

THE CHOROID RETE MIRABILE OF THE FISH EYE. II.  
DISTRIBUTION AND RELATION TO THE  
PSEUDOBRANCH AND TO THE  
SWIMBLADDER RETE  
MIRABILE.<sup>1</sup>

JONATHAN B. WITTENBERG<sup>2</sup> AND RICHARD L. HAEDRICH

*The Department of Physiology, Albert Einstein College of Medicine, New York, New York 10461; The Marine Biological Laboratory, Woods Hole, Massachusetts 02543; and The Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543*

The choroid rete mirabile is a large discrete organ lying within the eyeball behind the retina of many fishes. It is made up of several thousand closely arrayed and parallel arterial and venous capillaries in which the afferent and efferent blood streams flow counter-current one to another. This organ supplies arterial blood to the choriocapillaris (the dense capillary network underlying the retina), and in turn receives the venous outflow from these capillaries (Barnett, 1951). Probably in conjunction with the pigment cell epithelium, the choroid rete acts to maintain a large pressure of oxygen at the retina (Wittenberg and Wittenberg, 1962, 1974).

This investigation was undertaken to determine whether the distribution of the choroid rete mirabile in fishes is correlated with habitat, and, in particular, whether it is to be found in deep-living fishes. We find the choroid rete in both shallow- and deep-living fishes, and conclude that the ability to do without a choroid rete typifies families or orders of teleosts. Within such families or orders, the entire group, particular subgroups or individual genera, may lack the choroid rete.

Among non-teleosts, the rete is present only in *Amia*; this may represent either an independent or a convergent evolutionary development. Within certain broad teleostean groupings, presence or, more particularly, absence of the choroid rete may indicate phylogenetic relationships. Two diverse, unrelated teleostean groups in which the choroid rete is absent are the eels (Anguilloidei) and the wholly deep-sea suborder Stomiatoidei. In the Scopelomorpha, the choroid rete is present in all families except the Myctophidae, emphasizing a dichotomy within the suborder recently predicated on other characters by Rosen and Patterson (1969). For the most part, however, presence or absence of the rete as a character should be used by evolutionists with the greatest care, and then only in a supporting role. We find it too widely spread, and perhaps too easily lost, to be of much use in unscrambling the complicated and intricate phylogeny of fishes.

<sup>1</sup> This investigation was supported in part by Research Grants G 20020 and GB 20981 from the United States National Science Foundation and by a United States Public Health Research Grant, H3719, from the National Heart Institute. Contribution number 2722 from the Woods Hole Oceanographic Institution.

<sup>2</sup> Research Career Program Awardee 01-HL6-733 of the United States Public Health Service, National Heart and Lung Institute.

TABLE I

*Cyclostomes and elasmobranchs examined, none have a choroid rete mirabile.*

Agnatha	Myxiniiformes
Hagfish	<i>Myxine glutinosa</i> *
Sea lamprey	Petromyzontiformes
Brook lamprey	<i>Petromyzon marinus</i> **
Chondrichthyes	<i>Lampetra fluviatilis</i> ***
Bigeye thresher shark	Squaliformes
White shark	<i>Alopias superciliosus</i>
Smooth dogfish	<i>Carcharodon carcharias</i>
Spiny dogfish	<i>Mustelus canis</i>
Torpedo ray	<i>Squalus acanthias</i>
Winter skate	<i>Torpedo nobiliana</i>
Sting ray	<i>Raja ocellata</i>
Chimaera	<i>Dasyatis centroura</i>
	Chaemaeriformes
	<i>Hydrolagus collicii</i>

\* Not examined. The eye is very much reduced; there is no choroid rete mirabile (Ross, 1963).

\*\* Eyes and pineal eye examined.

\*\*\* N. A. Lockett, Institute of Ophthalmology, London, private communication.

The pseudobranch, a modified gill, sits astride the blood supply to the eye, and arterial blood destined for the choroid rete must pass first through its capillaries. The oxygen-concentrating mechanism of any rete mirabile inevitably must also concentrate all diffusible substances for which there is a "primary concentrating effect." These include carbon dioxide present in the incoming blood. We advance the suggestion that the pseudobranch acts to modify the incoming arterial blood in such a way that the counter-current multiplication system of the choroid rete may concentrate oxygen without simultaneously building up an untoward concentration of carbon dioxide within the eye. Carbon dioxide when hydrated becomes a strong acid. The pattern of occurrence of the pseudobranch among salt, brackish, and fresh-water fishes provides a clue as to how this major function of the pseudobranch is accomplished.

#### MATERIALS AND METHODS

Eyes from specimens in museum or other collections were fixed for the most part in neutral formaldehyde and stored in 40 per cent isopropanol or 70 per cent ethanol. Eyes from fresh specimens were fixed in acid formalin (formalin, 10 volumes, glacial acetic acid, 5 volumes, water to 100 volumes) and were later transferred to 70 per cent ethanol. Histological sections were prepared from eyes transected in the saggital or horizontal plane. When the eye was small, serial sections were made. Identification of the choroid rete mirabile in most instances rests on both its gross appearance in dissected specimens and on its characteristic microscopic structure as seen in section. In all cases reported, the identification was unequivocal; particular care was taken not to miss an inconspicuous structure when the rete appeared to be absent. Except as noted, all statements that the rete

is present or absent rest on our original observations. In the early and extensive studies of Brauer (1902, 1908), the choroid rete is not discussed, but is shown in his figures where it is identified as a "blood vessel" ("Blutgefäß").

The pseudobranch when present is usually easily visible on the inner face of the opercle. In the Gadiformes, Atheriniformes and in occasional genera (*e.g.*, *Esox*, *Echeneis*, *Coryphaena*) of other groups, the pseudobranch is not evident to casual inspection but is revealed by dissection. The identity of the pseudobranch in these fishes was confirmed by histological examination. In some fresh water groups (*e.g.*, Characidae) the pseudobranch is small and is found only with difficulty. For this reason, it is occasionally difficult to be absolutely certain that a particular species lacks the pseudobranch. No dubious cases are included in Table VI.

We follow the recent classification of teleosts of Greenwood, Rosen, Weitzman and Meyers (1966), with the modifications of Greenwood, Myers, Rosen and Weitzman (1967), of Rosen and Patterson (1969), of Rosen and Greenwood (1970), and of Greenwood and Rosen (1971). We follow the phyletic relations of the sarcopterygian, chondrosteian and holostean groups as given by Nelson (1969a, 1969b). Common names of fishes are those of Bigelow and Schroeder (1953) and the American Fisheries Society (1960).

#### RESULTS AND DISCUSSION

There is no choroid rete mirabile in the eye of hagfish, lampreys, nor in the eyes of sharks, skates, rays, and chimaeras (Table I).

There is no choroid rete mirabile in the eyes of the lobe-finned fishes *Polypterus*, *Calamoichthys*, *Latimeria*, and the lungfishes *Protopterus*, *Lepidosiren*, and *Neo-*

TABLE II

*Bony fishes examined other than teleosts. Of those here, only Amia has a choroid rete mirabile.*

Sarcopterygii	Brachiopterygii
Bichir	<i>Polypterus unatipinnis</i>
Reedfish	<i>Calamoichthys calabaricus</i>
Coelacanth	Coelacanthini
African lungfish	<i>Latimeria chalumnae*</i>
South american lungfish	Dipnoi
Australian lungfish	<i>Protopterus aethiopicus</i>
Actinopterygii	<i>Lepidosiren paradoxa</i>
Sturgeon	<i>Neoceratodus forsteri</i>
Paddlenosed sturgeon	Chondrostei
Paddlefish	<i>Acipenser oxyrhynchus</i>
Gar	<i>Scaiphirhynchus platyrhynchus</i>
Bowfin	<i>Polyodon spathula</i>
	Holostei
	<i>Lepisosteus osseus</i>
	<i>Amia calva</i>

\* See text.

*ceratodus* (Table II). Munk (1964, 1968b, 1969b) describes the structure of the eyes of some of these and compares them with *Amia*, *Lepisosteus* and teleosts.

The eye of the coelacanth, *Latimeria chalumnae*, was not examined in this study. The eye has been described briefly by Millot and Carasso (1955) and by Millot and Anthony (1958a). Millot and Anthony (1958b, plates VI and XIV; 1965, plates LVIII and LX) present photographs of the eye transected in planes which would be expected to include the rete were it present; there is none visible. Dr. N. A. Locket, Institute of Ophthalmology, University of London (private communication) has examined a coelacanth eye which had been divided sagittally; there is no suggestion of a rete, and histological sections confirm this observation.

There is no choroid rete mirabile in the eyes of the chondrosteans, sturgeons and the paddlefish (Table II).

There are two living holosteans, the gar and the bowfin. Of these, the gar, *Lepisosteus*, has no choroid rete. The bowfin, *Amia calva*, however, does, and is the only non-teleost fish we have found to have one (Table II). Wittenberg and Wittenberg (1974) describe the architecture of this rete. The structure of the holostean eye is described most recently by Munk (1968b). The rete of *Amia* may represent an independent evolutionary development convergent with that of the teleosts. On the other hand, it is equally possible that a common ancestor of *Amia* and of the teleosts may either have developed a choroid rete mirabile or had the genetic capability to develop one. Whether *Amia* and teleosts share an immediate common ancestor is at present a matter of debate; see a discussion by Nelson (1969a, 1969b). However this question is resolved, the choroid rete of *Amia* serves the same function as that of the teleosts—to maintain a large pressure of oxygen at the retina (Wittenberg and Wittenberg, 1974).

The choroid rete mirabile is widely distributed among teleosts (Table III). It is nearly ubiquitous among the Acanthopterygii which make up the great majority of living forms. It is lacking in eels (Anguilloidei) which are unique among fishes in having vascular retinas (Duke-Elder, 1958; Walls, 1942), possibly obviating the need for a choroid rete.

The Gadiformes present an instructive diversity. This group includes members, for example the cod, haddock, pollack, and silver hake, with powerfully-developed choroid retia. On the other hand, the rete is reduced to a minute, although certainly functional, structure in the three morids examined. These are relatively deep to very deep-living animals. The macrurids, typically deep-living forms, carry this tendency a step further; the rete of *Nezumia* is reduced in size almost to the vanishing point, while the other two species examined lack retia altogether. Two zoarcids were examined; the shallow-living *Macrozoarces* was found to have a normal-sized rete, while the deep-living *Lycodes*, captured from 1400 meters lacks a rete. One cannot, on this evidence, conclude that life at depth is the sole reason for loss of the rete—the two shallow-living ophidiids, *Lepophidium* and *Otophidium*, lack retia, as does their deep-living relative, *Dicrolene*. A more conservative conclusion is that the Gadiformes have the potential to do without the choroid rete. When it has selective advantage, the rete is powerfully developed, but it becomes reduced in species subject to selective pressures favoring its loss.

The loss of, or the ability to lose, the choroid rete is a character typifying certain families or larger groupings. Contrast, for instance, the stomiatoids, nearly

TABLE III

Distribution of the choroid rete mirabile and pseudobranch in teleosts. Plus indicates organ present. Zero indicates organ absent. Specimens not examined are designated n.e.

DIVISION I (TAENIOPAEDIA)			Choroid Rete	Pseudo-branch
	Superorder Elopomorpha			
	Order Elopiformes			
	Suborder Elopoidei			
Ladyfish	Elopidae	<i>Elops saurus</i>	+	+
		<i>Elops affinis</i>	n.e.	+
Tarpon	Megalopidae	<i>Megalops atlantica</i>	+	+
		<i>Megalops cyprinoides</i>	+	+
	Suborder Albuloidae			
Bonefish	Albulidae	<i>Albula vulpes</i>	+	+
		<i>Pterothrissus gissu</i>	n.e.	+
		<i>Dixonia nemoptera</i>	+	+
	Order Anguilliformes			
	Suborder Anguilloidei			
American eel	Anguillidae	<i>Anguilla rostrata</i>	0	n.e.
Conger	Congridae	<i>Conger oceanicus</i>	0	n.e.
Moray	Muraenidae	<i>Muraena</i> sp.	0	n.e.
Snipe eel	Nemichthyidae	<i>Nemichthys scolopaceus</i>	0	n.e.
Longnose eel	Synphobranchidae	<i>Synphobranchus pinnatus</i>	0	n.e.
	Order Notacanthiformes			
	Halosauridae	<i>Aldrovandia phalacra</i>	0	0
Spiny eel	Notacanthidae	<i>Notacanthus</i> sp.	0	0
		<i>Polyacanthonotus rissouan</i>	0	0
	Superorder Clupeomorpha			
	Order Clupeiformes			
	Suborder Clupeoidei			
Anchovy	Engraulidae	<i>Anchoa mitchilli</i>	+	+
Hickory shad		<i>Alosa mediocris</i>	+	+
Alewife		<i>Alosa pseudoharengus</i>	+	+
Menhaden		<i>Brevoortia gunteri</i>	+	+
Menhaden		<i>Brevoortia tyrannus</i>	+	+
Herring	Clupeidae	<i>Clupea harengus</i>	+	+
DIVISION II (ARCHAEOPHYLACES)				
	Superorder Osteoglossomorpha			
	Order Osteoglossiformes			
	Suborder Osteoglosioidei			
Aruana	Osteoglossidae	<i>Osteoglossum bicirrhosum</i>	+	0
		<i>Heterotis niloticus</i>	+	0
		<i>Scleropages guentheri</i>	+	0
Arapaima		<i>Arapaima gigas</i>	+	0
		<i>Scleropages formosus</i>	+	n.e.
Butterfly fish	Pantodontidae	<i>Pantodon buchholzi</i>	+	0
	Suborder Notopteroidei			
Goldeye	Hiiodontidae	<i>Hiiodon alosoides</i>	+	0
Featherback	Notopteridae	<i>Notopterus notopterus</i>	+	0
Featherback		<i>Notopterus chitala</i>	+	0
African knife fish		<i>Xenomystus nigri</i>	+	0
	Order Mormyriiformes			
	Mormyridae	<i>Gnathonemus tomamura</i>	0	n.e.
		<i>Gnathonemus petersii</i>	0	0
		<i>Gnathpneustes niger</i>	0	0
		<i>Gymnarchus niloticus</i>	0	0
	Gymnarchidae			
DIVISION III (EUTELEOSTEI)				
	Superorder Protacanthopterygii			
	Order Salmoniformes			
	Suborder Salmonoidei			
Whitefish	Salmonidae	<i>Coregonus clupeaformis</i>	+	+
Brown trout		<i>Salmo trutta</i>	+	+
Grayling		<i>Thymallus thymallus</i>	+	n.e.
Smelt		<i>Osmerus mordax</i>	+	+
Capelin	Osmeridae	<i>Mallotus villosus</i>	+	n.e.

TABLE III—Continued

DIVISION III (EUTELEOSTEI)—Continued			Choroid Rete	Pseudo-branch	
Argentine Argentine	Suborder Argentinoidei				
	Argentiniidae	<i>Argentina silus</i>	+	n.e.	
		<i>Argentina sphyraena</i>	+	n.e.	
		<i>Nansenia groenlandica</i> <sup>b</sup>	+	n.e.	
	Bathylagidae	<i>Bathylagus pacificus</i> <sup>b</sup>	+	n.e.	
		<i>Bathylagus stilbius</i> <sup>b</sup>	+	n.e.	
		<i>Bathylagus longirostris</i>	+	+	
		<i>Bathylachnops exilis</i> <sup>b</sup>	+	n.e.	
		<i>Opisthoproctus grimaldii</i> <sup>b</sup>	+	n.e.	
		<i>Rhynchohyalus natalensis</i> <sup>c</sup>	+	n.e.	
		<i>Winteria telescopa</i> <sup>b</sup>	+	+	
		<i>Alepocephalus agassizi</i>	+	+	
		<i>Platyroctegus mirus</i> <sup>b</sup>	+	n.e.	
		<i>Bathylaco nigricans</i> <sup>d</sup>	+	+	
	Hatchetfishes	Suborder Stomiatoidei			
Gonostomatidae		<i>Gonostoma elongatum</i> <sup>b,e</sup>	0	0	
		<i>Vinciguerria poweriac</i>	0	0	
Sternoptychidae		<i>Argyropelecus</i> sp. <sup>e</sup>	+	n.e.	
		<i>Argyropelecus aculeatus</i>	n.e.	+	
		<i>Argyropelecus olfersi</i> <sup>b</sup>	0	+	
		<i>Sternoptyx</i> sp. <sup>e</sup>	+	+	
Astronesthidae		<i>Astronesthes indicus</i> <sup>b</sup>	0	n.e.	
		<i>Astronesthes niger</i>	0	0	
		<i>Borostomias antarcticus</i>	0	0	
Melanostomiidae		<i>Bathophilus pawneeii</i> <sup>b</sup>	0	n.e.	
		<i>Bathophilus metallicus</i> <sup>b</sup>	0	0	
		<i>Eustomias obscurus</i> <sup>b</sup>	0	0	
		<i>Flagellostomias bourceii</i> <sup>b</sup>	0	n.e.	
		<i>Melanostomias spilorhynchus</i> <sup>b</sup>	0	0	
Viperfishes	Malacosteidae	<i>Malacosteus niger</i>	0	0	
	Chauliodontidae	<i>Chauliodon schmidti</i>	0	0	
		<i>Chauliodon sloani</i> <sup>b</sup>	0	0	
		<i>Chauliodon</i> sp. <sup>e</sup>	0	n.e.	
		<i>Stomias</i> sp. <sup>b</sup>	0	n.e.	
		<i>Stomias boa</i>	n.e.	0	
		<i>Idiacanthus fascicola</i> <sup>b</sup>	0	0	
		Suborder Esocoidei			
		Esocidae	<i>Esox niger</i>	+	0
		Umbridae	<i>Umbrina limi</i>	+	0
Pickerel Mud minnow	Superorder Ostariophysii				
	Series Anotoptysi				
	Order Gonorynchiformes				
	Suborder Chanoidei				
	Channidae	<i>Chanos chanos</i>	+	+	
	Series Otophysi				
	Order Cypriniformes				
	Suborder Characoidei				
	Characidae	<i>Alestes kingsleyae</i>	+	+	
		<i>Brycon striatulus</i>	+	+	
	<i>Creatochanes melanurus</i>	+	+		
	<i>Serrasalmus nattereri</i>	+	+		
Piranha South American knifefish	Gymnotidae	<i>Eigenmannia virescens</i>	0	0	
	Apteronotidae	<i>Sternarchus albifrons</i>	0	0	
	Suborder Cyprinoidei				
	Cyprinidae	<i>Cyprinus carpio</i>	+	n.e.	
		<i>Carassius auratus</i>	+	n.e.	
		<i>Tinca vulgaris</i>	+	+	
		<i>Catostomus commersoni</i>	+	+	
		Order Siluriformes			
		Ictaluridae	<i>Ameriurus nebulosus</i>	0	n.e.
		Bagridae	<i>Bagrus docmac</i>	0	n.e.
		<i>Bagrus marinus</i>	0	0	
Catfish Catfish Gafftopsail catfish Walking catfish	Clariidae	<i>Clarias batrachus</i> <sup>o</sup>	0	n.e.	
	Superorder Scopelomorpha				
	Order Myctophiformes				
	Synodontidae	<i>Synodus fortans</i>	+	+	
		<i>Synodus</i> sp.	+	+	
		<i>Omosudis lowei</i> <sup>b,t</sup>	+	+	
		<i>Alepisaurus brevirostris</i>	+	+	
		<i>Evermannella indica</i> <sup>b</sup>	+	+	
	Lizardfish Lanternfish	Omosudidae			
		Alepisauridae			
Evermannellidae					

TABLE III—Continued

DIVISION III (EUTELEOSTEI)—Continued			Choroid Rete	Pseudo-branch
	Scopelarchidae	<i>Neoscopelarchoides</i> sp. <sup>b</sup>	+	+
		<i>Scopelarchus</i> sp. <sup>a</sup>	+	+
Lanternfishes	Myetophidae	<i>Ceratoscopelus maderensis</i>	0	+
		<i>Lampanyctus macdonaldi</i>	0	+
		<i>Myctophum punctatum</i>	0	+
		<i>Symbolophorus veranyi</i>	0	+
		<i>Scopelengys tristis</i>	0	0
	Neoscopelidae			
	Superorder Paracanthopterygii			
	Series Polymixiomorpha			
	Order Polymixiiformes			
Beardfish	Polymixiidae	<i>Polymixia nobilis</i>	+	+
	Series Salmopercomorpha			
	Order Percopsiformes			
Troutperch	Percopsidae	<i>Percopsis omiscomaycus</i>	+	+
	Order Gadiformes			
	Suborder Gadoidei			
Blue hake	Moridae	<i>Antimora rostrata</i>	+	0
		<i>Halargyreus johnsonii</i>	+	0
		<i>Mora moro</i>	+	n.e.
Cod	Gadidae	<i>Gadus morhua</i>	+	+
Freshwater cod		<i>Lota lota</i>	+	n.e.
Haddock		<i>Melanogrammus aeglefinus</i>	+	n.e.
Tomcod		<i>Microgadus tomcod</i>	+	n.e.
Pollack		<i>Pollachius virens</i>	+	+
Rockling		<i>Enchelyopus cimbrius</i>	+	+
Longfin hake		<i>Urophycis chesteri</i>	+	+
Squirrel hake		<i>Urophycis chuss</i>	+	+
Spotted hake		<i>Urophycis regia</i>	+	+
White hake		<i>Urophycis tenuis</i>	+	n.e.
Silver hake (whiting)		<i>Merluccius bilinearis</i>	+	+
	Merlucciidae			
	Suborder Macrouroidei			
	Macrouridae	<i>Nezumia bairdii</i>	+	+
		<i>Macrurus</i> sp.	0	n.e.
		<i>Macrurus tenuicauda</i>	0	n.e.
	Suborder Ophidioidei			
	Ophidiidae	<i>Dicrolene intronigra</i>	0	0
Cusk eel		<i>Lepophidium certinum</i>	0	+
Cusk eel		<i>Otophidium welshi</i>	0	0
	Suborder Zoarcoidei			
	Zoarcaeidae	<i>Macrozoarces americanus</i>	+	+
Ocean pout		<i>Lycodes atlanticus</i>	0	0
Eel pout				
	Order Batrachoidiformes			
	Batrachoididae	<i>Opsanus tau</i>	+	0
Toadfish		<i>Ogcocephalus nasutus</i>	+	n.e.
Batfish		<i>Porichthys notatus</i>	0	+
Midshipman				
	Order Lophiiformes			
	Suborder Lophioidei			
	Lophiidae	<i>Lophius piscatorius</i>	+	0
Goosefish				
	Suborder Antennarioidei			
	Antennariidae	<i>Histrio pictus</i>	+	n.e.
Sargassum fish				
	Suborder Ceratioidei			
	Ceratiidae	<i>Cerattias holboellii</i> <sup>b</sup>	0	n.e.
Deep sea anglerfish		<i>Cryptopsaras cousti</i> <sup>b</sup>	0	n.e.
		<i>Linophrync arborifer</i> <sup>b</sup>	0	n.e.
	Linophrynidae			
	Superorder Acanthopterygii			
	Series Atherinomorpha			
	Order Atheriniiformes			
	Suborder Exocoetoidei			
	Exocoetidae	<i>Exocoetus</i> sp.	+	n.e.
Flying fish		<i>Oxyporhamphus micropterus</i>	+	+
Flying fish		<i>Danichthys rondeletti</i>	+	+
Flying fish		<i>Hyporhamphus unifasciatus</i>	+	+
Halfbeak		<i>Petalichthys capensis</i>	+	+
		<i>Strongylura</i> sp.	+	n.e.
Houndfish		<i>Tylosurus acus</i>	+	+
Needlefish				
	Scomberesocidae			
Saury		<i>Somberesox saurus</i>	+	0
	Suborder Cyprinodontoidae			
	Cyprinodontidae	<i>Cyprinodon variegatus</i>	+	+
Sheepshead minnow		<i>Fundulus heteroclitus</i>	+	+
Mummichog		<i>Fundulus majalis</i>	+	+
Mummichog		<i>Xiphophorus</i> sp.	+	+
Platy		<i>Aplocheilichthys lineatus</i> <sup>a</sup>	+	+
		<i>Epiplatys grahami</i> <sup>a</sup>	+	+

TABLE III—Continued

DIVISION (III EUTELEOSTEI)—Continued			Choroid Rete	Pseudo-branch
Foureyes	Anablepidae	<i>Anableps tetropthalmus</i> <sup>b</sup>	+	n.e.
Opah	Series Percomorpha			
	Order Lampridiformes			
	Lampridae	<i>Lampris regius</i>	+	n.e.
	Suborder Stylephoroidei			
	Stylephoridae	<i>Stylephorus chordatus</i> <sup>b</sup>	+	n.e.
	Order Beryciformes			
	Suborder Stephanoberycoidei			
	Melamphaeidae	<i>Poromitra nigrofulvus</i> <sup>c</sup>	0	n.e.
		<i>Scopelogadus beanii</i>	0	0
	Suborder Berycoidei			
	Diretmidae	<i>Diretmus argenteus</i> <sup>d</sup>	+	n.e.
American john dory	Order Zeiformes			
	Zeidae	<i>Zenopsis ocellata</i>	+	+
	Order Gasterosteiformes			
Stickleback	Suborder Gasterosteoidae			
	Gasterosteidae	<i>Gasterosteus aculeatus</i>	+	+
	Suborder Aulostomoidei			
Cornet fish	Fistulariidae	<i>Fistularia tabacaria</i>	+	+
	Suborder Syngnathoidei			
Seahorse	Syngnathidae	<i>Hippocampus hudsonius</i>	+	n.e.
Pipefish		<i>Syngnathus louisianae</i>	+	n.e.
	Order Channiformes			
Snakehead	Channidae	<i>Ophicephalus micropeltes</i>	+	0
Snakehead		<i>Channa asiatica</i>	+	0
	Order Scorpaeniformes			
	Suborder Scorpaenoidei			
	Scorpaenidae	<i>Helicolenus dactylopterus</i>	+	+
Blackbelly rosefish		<i>Scorpaena brasiliensis</i>	+	+
Scorpion fish		<i>Sebastes marinus</i>	+	+
Rosefish		<i>Prionotus carolinus</i>	+	+
Sea robin	Triglidae			
	Suborder Cottoidei			
	Cottidae	<i>Cottunculus microps</i>	0	0
Arctic sculpin		<i>Hemitrypterus americanus</i>	+	+
Sea raven		<i>Myoxocephalus octodecimspinosus</i>	+	+
Longhorn sculpin		<i>Cyclopterus lumpus</i>	+	+
Lumpfish	Cyclopteridae			
	Order Perciformes			
	Suborder Percoidei			
	Percichthyidae	<i>Polyprion americanus</i>	+	+
Wreckfish		<i>Morone saxatilis</i>	+	+
Striped bass		<i>Centropristis striatus</i>	+	+
Sea bass	Serranidae	<i>Diplectrum formosum</i>	+	+
Sand perch				
Sunfish	Centrarchidae	<i>Lepomis auritus</i>	+	+
Crappie		<i>Pomoxis annularis</i>	+	+
Largemouth bass		<i>Micropterus salmoides</i>	+	+
Yellow perch	Percidae	<i>Perca flavescens</i>	+	+
Walleye		<i>Stizostedion vitreum</i>	+	+
	Branchiostegidae			
Tilefish		<i>Lopholatilus chamaeleonticeps</i>	+	n.e.
Bluefish	Pomatomidae	<i>Pomatomus saltatrix</i>	+	+
Remora	Echeneidae	<i>Echeneis naucrates</i>	+	+
Bigeye scad	Carangidae	<i>Selar crumenophthalmus</i>	+	+
Dolphin	Coryphaenidae	<i>Coryphaena equiselis</i>	+	0
Black pomfret	Apolectidae	<i>Apolectus niger</i>	+	+
Snapper	Lutjanidae	<i>Etelis marshi</i> <sup>c</sup>	+	n.e.
Scup, porgy	Sparidae	<i>Stenotomus versicolor</i>	+	+
Sand seatrout	Sciaenidae	<i>Cynoscion arenarius</i>	+	+
Salt water drum		<i>Micropogon undulatum</i>	+	+
Fresh water drum		<i>Aplodinotus grunniens</i>	+	+
Spotted seatrout		<i>Cynoscion nebulosus</i>	+	+
Minkfish		<i>Menticirrhus focaliger</i>	+	+
Kingfish		<i>Menticirrhus saxatilis</i>	+	n.e.
Spadefish		<i>Chaetodipterus faber</i>	+	+
	Ephippidae			
	Suborder Mugiloidei			
Mullet	Mugilidae	<i>Mugil cephalus</i>	+	+
	Suborder Sphyraenoidei			
Northern barracuda	Sphyraenidae	<i>Sphyraena borealis</i>	+	+
Barracuda		<i>Sphyraena</i> sp.	+	n.e.
	Suborder Labroidei			
Tautog	Labridae	<i>Tautoga onitis</i>	+	+
Cunner		<i>Tautoglabrus adspersus</i>	+	+



TABLE III—Continued

DIVISION III (EUTELEOSTEI)—Continued			Choroid Rete	Pseudo-branch
Redtail parrotfish	Scaridae	<i>Sparisoma chrysopterym</i>	+	+
	Suborder Trachinoidei			
	Chiasmodontidae	<i>Chiasmodon</i> sp.	+	+
Icefishes	Suborder Notothenioidei			
	Nototheniidae	<i>Notothenia cornucola</i>	+	n.e.
		<i>Harpagifer bispinus</i>	0	n.e.
		<i>Chaenocephalus aceratus</i>	0	n.e.
		<i>Champsoccephalus gunnari</i>	0	n.e.
Florida blenny Wolffish Foureyed blenny Wrymouth Rock gunnel Shanny	Suborder Blennioidei			
	Blenniidae	<i>Chasmodes sabburac</i>	+	+
	Anarhichadidae	<i>Anarhichus lupus</i>	+	+
	Clinidae	<i>Dialommus fuscus</i> <sup>b</sup>	+	n.e.
	Stichaeidae	<i>Cryptacanthodes maculatus</i>	0	n.e.
		<i>Pholis gunnellus</i>	+	+
		<i>Leptoclinius maculatus</i>	+	+
	Suborder Scombroidei			
	Gempylidae	<i>Thyrsites atun</i>	+	+
		<i>Ruvettus pretiosus</i>	+	+
Oilfish	Scombridae			
		<i>Lepidocybium flavobrunneum</i>	+	+
		<i>Sarda sarda</i>	+	+
		<i>Scomber scombrus</i>	+	+
		<i>Scomberomorus cavalla</i>	+	n.e.
	<i>Thunnus thynnus</i>	+	+	
White marlin Swordfish	Istiophoridae	<i>Makaira albidia</i>	+	n.e.
	Xiphiidae	<i>Xiphus gladius</i>	+	+
Barrel fish Butterfish Harvest fish	Suborder Stromateoidei			
	Centrolophidae	<i>Hyperoglyphe bythites</i>	+	+
	Stromateidae	<i>Peprilus triacanthus</i>	+	+
		<i>Peprilus alepidotus</i>	+	n.e.
		<i>Ariomma regulus</i>	+	+
Climbing perch Gourami	Suborder Anabantoidi			
	Anabantidae	<i>Anabas oligolepis</i>	+	0
	Helostomatidae	<i>Helostoma temmincki</i>	+	0
Winter flounder Yellow tail flounder Sand flounder Fluke	Order Pleuronectiformes			
	Suborder Pleuronectoidei			
	Pleuronectidae	<i>Pseudopleuronectes americanus</i>	+	+
		<i>Limanda ferruginea</i>	+	+
		<i>Lophopsetta maculata</i>	+	+
	<i>Paralichthys dentatus</i>	+	+	
File fish	Order Tetraodontiformes			
	Suborder Balistoidei			
	Balistidae	<i>Monacanthus hispidus</i>	+	+
Puffer Cowfish Spiny boxfish Striped burrfish Ocean sunfish	Suborder Tetraodontoidei			
	Tetraodontidae	<i>Sphaeroides maculata</i>	+	+
		<i>Lactrophrys tricorns</i>	+	n.e.
		<i>Diodon hystrix</i>	+	n.e.
		<i>Chilomycterus schopfi</i>	+	n.e.
	Molidae	<i>Mola mola</i>	+	n.e.

Notes to Table III:

- <sup>a</sup> McDowell (1973) finds that the pseudobranch is absent throughout this order. We confirm his finding for *Aldrovandia* and *Notacanthus*; we did not examine the pseudobranch of *Polyacanthonotus*.
- <sup>b</sup> Rete or its absence noted by Munk (1966a).
- <sup>c</sup> Rete noted by Bertelsen, Theisen and Munk (1965).
- <sup>d</sup> Rete noted by Munk (1968a).
- <sup>e</sup> Rete or its absence noted by N. A. Locket, private communication.
- <sup>f</sup> Rete noted by Munk (1965).
- <sup>z</sup> Rete noted by Munk (1970). Pseudobranch described by Poernomo (1967).
- <sup>h</sup> Rete noted by Arruga, quoted in Duke-Elder (1958).
- <sup>i</sup> Rete noted by Munk (1966b).
- <sup>j</sup> Rete noted by Munk (1969a).

all of which lack the choroid rete, with the other suborders of Salmoniformes, nearly all of which have choroid retia. The Salmoniformes are for the most part small mesopelagic animals, presumably living somewhat similar lives. Another clear example is encountered in the Scopelomorpha, where six families have the rete, and a single family, the speciose Myctophidae, lacks the rete.

The Notothenioids deserve comment. The two chaenichthyids studied are examples of the famous icefishes described by Ruud (1965) as having neither red

blood cells nor hemoglobin in their blood. Also absent are swimbladders (Rüüd, private communication) and choroid retia. It cannot be said whether the loss of these structures is secondary to the loss of red blood cells. In an attempt to find out, the eyes of two related nototheniids were examined. At least one of these, *Notothenia*, is known to have red blood (Tyler, 1960) and has a choroid rete. Another, *Harpagifer*, lacks the choroid rete.

We discuss next the relation between the occurrence of retia in the swimbladder and the eye. The retia of the swimbladder and of the eye are similar both in structure and in one known function—to secrete oxygen. The question arises whether species which dispense with one or the other of these structures do so because of some aspect of their physiology or their habitat which makes the operation of a counter-current organ ineffective. Table IV lists some fish lacking the

TABLE IV  
*Fish lacking choroid retia but having well-developed swimbladder retia  
or oxygen secretion into the swimbladder.*

		Reference to Swimbladder
Eel	<i>Anguilla rostrata</i>	Fänge and Wittenberg, 1958
Conger	<i>Conger oceanicus</i>	Richard, 1895
Moray	<i>Muraena helena</i>	Schloesing and Richard, 1896
Longnose eel	<i>Synaphobranchus pinnatus</i>	Schloesing and Richard, 1896
Spiny eels	<i>Notacanthiformes</i>	McDowell, 1973
	<i>Vinciguerria</i> sp.	Kanwisher and Ebeling, 1957
	<i>Argyropelecus olfersi</i>	Marshall, 1960
	<i>Astronesthes niger</i>	Marshall, 1960
	<i>Ceratoscopelus maderensis</i>	Backus <i>et al.</i> , 1968
	<i>Lampanyctus</i> sp.	Marshall, 1960
	<i>Myctophium</i> sp.	Kanwisher and Ebeling, 1957
		Marshall, 1960
	<i>Porichthys notatus</i>	This work
	<i>Dicrolene inronigra</i>	This work
	<i>Otophidium welshi</i>	This work
	<i>Macrurus</i> sp.	This work
	<i>Poromitra</i> sp.	Kanwisher and Ebeling, 1957

choroid rete but having well-developed swimbladder retia and oxygen secretion into the swimbladder. Table V lists some examples of the converse case, species with well-developed choroid retia but with the swimbladder rete poorly developed or seemingly absent. These fishes secrete oxygen into the swimbladder, but very slowly. From these observations, we conclude that the swimbladder rete and the choroid rete occur independently.

We discuss next the relation of the pseudobranch to the choroid rete mirabile. The pseudobranch is widely distributed among fishes and seldom lost. Those instances in which it is lost, therefore, offer an occasion for deductions about its function.

The pseudobranch is a modified (first, spiracular) gill arch which receives oxygenated blood from the first efferent gill artery and in turn gives rise to an artery of which the ophthalmic artery, supplying the choroid rete, is a main branch

(Allen, 1905; Allis, 1900, 1908, 1912, and references therein; Barnett, 1951; Müller, 1839; Prince, 1956). (Goodrich, 1930, and Prince, 1956, present useful figures.) Blood, passing from the heart to the eye and back to the heart passes through five tandem sets of capillaries as follows: the gill capillaries, the pseudo-branchial capillaries, and, within the eye, the afferent (arterial) capillaries of the choroid rete mirabile, the capillaries of the chorio-capillaris underlying the retina and lastly the efferent (venous) capillaries of the choroid rete.

In many teleost species, the pseudobranch retains the external appearance of a gill hemibranch, but is distinguished from a gill by its location on the inner face of the opercle, where it shares access to the respiratory current of water. In other species (*e.g.*, many gadoids), the filaments of the pseudobranch are to a greater or lesser extent fused, so that diffusion from blood to sea water must be substantially impeded, and respiratory exchange minimized. Such pseudobranchs are often covered by a flap or layer of epithelium. In still others, the respiratory filaments

TABLE V

*Fish with well-developed choroid retina but weakly-developed swimbladder  
retia or oxygen secretion into the swimbladder.*

		Reference to Swimbladder
Herring	<i>Clupea harengus</i>	Fahlén, 1967a
Smelt	<i>Osmerus mordax</i>	Fahlén, 1968
Capelin	<i>Mallotus villosus</i>	Fahlén, 1968
Whitefish	<i>Coregonus clupeaformis</i>	Fahlén, 1967b Sundness, 1963
Brown trout	<i>Salmo trutta</i> *	Wittenberg, 1958
Grayling	<i>Thymallus thymallus</i>	Fahlén, 1968
Argentine	<i>Argentina silus</i>	Fänge, 1958
Carp	<i>Cyprinus carpio</i>	Fänge and Mattisson, 1956 Wittenberg, 1958
Goldfish	<i>Carassius auratus</i>	Wittenberg, 1958
Swordfish	<i>Xiphias gladius</i>	This Work

\* The measured oxygen pressure in the eye of trout is large (Fairbanks, Hoffert and Fromm, 1969).

are fused completely and the pseudobranch is a compact structure buried in connective tissue beneath the buccal epithelium. Among teleosts both the compact, "glandular" (Granel, 1922) pseudobranch (as in *Fundulus*—Copeland and Dalton, 1958; Ritch and Philpott, 1969) and the "free" pseudobranch resembling a gill hemibranch (as in the flounder—Harb and Copeland, 1969) are characterized by a cell type, the pseudobranchial cell, with an unique and elaborate ultrastructure.

Pseudobranchs homologous (Goodrich, 1930; Müller, 1839) with that of teleosts are found in elasmobranchs and in the Actinopterygii, but are lacking in the Sarcopterygii (Goodrich, 1930). The pseudobranchs of *Amia* and of teleosts are distinguished from the foregoing by the presence of large granular acidophil cells which when characterized in the electron microscope may be called "pseudobranchial cells." The difference is sufficiently striking that Goodrich (1930, page 521) on the basis of observations in the light microscope, was led to conclude that the pseudobranch in teleosts and *Amia* seems "to have acquired a new

function . . . in addition to its original function." Electron microscopic examination of the large pseudobranch of the gar, *Lepisosteus*, which lacks the choroid rete, reveals that pseudobranch type cells are absent (Harb, 1969). Regrettably, the pseudobranch of *Amia*, the other holostean, has not yet been studied in the electron microscope. We are here concerned with the interplay between the pseudobranch and the choroid rete and limit the discussion to *Amia* and the teleosts.

The position of the pseudobranch, astride the blood supply to the choroid rete mirabile, and the ultrastructural architecture of its cells, suggest that it may serve to modify the arterial blood entering the ophthalmic artery.

The pseudobranch may be well-developed in teleosts which lack choroid retia. This, however, is unusual, and of the fishes examined, we find it only in certain marine fishes, notably the Myctophidae, *Argyrops leucus*, *Lepophidium cervinum*, and *Porichthys notatus*. In the myctophids, in particular, the pseudobranch is a conspicuous gill-like structure on the inside of the opercle. In our opinion, such an occasional situation indicates multiple functions for the pseudobranch. One such is known. The pseudobranch is proved to act as a chemoreceptor responsive to oxygen and carbon dioxide pressures of the incoming blood in tench (Laurent, 1967; Laurent and Dunel, 1964, 1966).

Every marine teleost (with exceptions noted) which lacks a pseudobranch also lacks the choroid rete. Instances are: many stomiatoids, some orphidioids and zoarcids and the deep-living arctic sculpin, *Cottunculus*. The apparent exceptions to this rule, *Opsanus*, *Lophius*, *Antimora* and *Halargyreus* can scarcely be considered to contradict it since the choroid rete in these forms is reduced almost to the vanishing point, and the oxygen pressure in the eye of *Opsanus* is not elevated (Wittenberg and Wittenberg, 1962, 1974).

All fish in which the choroid rete mirabile is well developed and in which the pseudobranch is absent, inhabit fresh water, Table VI. The Elopiformes, all of which have powerfully developed choroid retia, show a striking gradation in the size of the pseudobranch, Table VI. Those species which are primarily marine, *Elops*, *Albula*, *Dixonia* and *Pterothrissus*, have conspicuous, large pseudobranchs. The tarpon, *Megalops atlantica*, which lives at times in salt, brackish and fresh water, has a very small pseudobranch. Finally, the pseudobranch of the Australian species, *Megalops cyprinoides*, of which our specimens were captured in fresh water, and whose habitat may be confined to fresh water, is minute. Only a few stubby protuberances occupy the position where the pseudobranch would be found. We infer that a function of the pseudobranch which is required for the operation of the choroid rete mirabile may be dispensed with in fresh water.

We turn to the role of the pseudobranchs in oxygen secretion. The pseudobranch is not essential for oxygen secretion *per se*, neither in the swimbladder nor in the eye. Many fishes, for instance, the eels, *Anguilla*, *Conger*, *Muraena*, *Synphobranchus*, the Notacanthiformes (McDowell, 1973), the midshipman, *Porichthys*, the toadfish *Opsanus*, some stomatiatoids, e.g., *Vinciguerria* and *Astronesthes*, and probably also morids, ophidiids and macrurids have swimbladder oxygen secretion powerfully developed although they lack pseudobranchs. (Bilateral extirpation of the pseudobranch was found to depress gas secretion into the swimbladder of *Fundulus* (Copeland, 1951) but not of *Perca* (Maetz, 1956), whose larger size may have made pseudobranchectomy a less traumatic procedure.) In

a fresh water fish, the trout, *Salmo irideus*, the prior passage of blood through the pseudobranch is not necessarily required for oxygen secretion into the eye. A small area of the choriocapillaris is supplied with blood from an accessory counter-current exchange structure, the lentiform body, which receives blood from the general circulation by way of the retinal artery (Barnett, 1951).

The blood supply to the major counter-current exchange structure, the choroid rete, can be cut off by extirpation of the pseudobranch: the oxygen pressure in the ipsilateral eye nevertheless remains significantly elevated above arterial oxygen pressure, through action of the lentiform body (Fairbanks, Hoffert and Fromm, 1969).

TABLE VI  
*Relation of the pseudobranch to the choroid rete mirabile*

		Pseudobranch	Habitat
	Order Elopiformes		
Ladyfish	<i>Elops saurus</i>	Large	Seawater
Machete	<i>Elops affinis</i>	Large	Seawater
Tarpon	<i>Megalops atlantica</i>	Very small	Brackish to fresh
	<i>Megalops cyprinoides</i>	Minute	Freshwater
Bonefish	<i>Albula vulpes</i>	Large	Seawater
	<i>Dixonia nemoptera</i>	Large	Seawater
	<i>Pterothrissus gissu</i>	Large	Seawater
	Order Osteoglossiformes		
Aruana	<i>Osteoglossum bicirrhosum</i>	Absent	Freshwater
Arapaima	<i>Arapaima gigas</i>	Absent	Freshwater
	<i>Heterotis niloticus</i>	Absent	Freshwater
	<i>Scleropages guentheri</i>	Absent	Freshwater
Butterflyfish	<i>Pantodon buchholzi</i>	Absent	Freshwater
Goldeye	<i>Hiodon alosoides</i>	Absent	Freshwater
Featherback	<i>Notopterus notopterus</i>	Absent	Freshwater
Featherback	<i>Noropterus chitala</i>	Absent	Freshwater
African knife-fish	<i>Xenomystus nigri</i>	Absent	Freshwater
	Order Salmoniformes		
	Suborder Esocoidei		
Mudminnow	<i>Umbra limi</i>	Absent	Freshwater
	Order Channiformes		
Snakehead	<i>Ophicephalus micropeltes</i>	Absent	Freshwater
Snakehead	<i>Channa asiatica</i>	Absent	Freshwater
	Order Perciformes		
Climbing perch	<i>Anabas oligolepis</i>	Absent	Freshwater
Gourami	<i>Helostoma temmincki</i>	Absent	Freshwater

We seek to discover the special constraints on the functioning of the choroid rete which require the presence of the pseudobranch. We note that the choroid rete secretes into a fluid-filled space, and any materials there concentrated must remain, except as they are removed by ancillary vascular circulation. The gas space of the swimbladder, on the other hand, allows transient accumulations of gases to be diluted by expansion into its volume. In many species an elaborate accessory circulation carries away transient and steady state accumulations of carbon dioxide and other gases.

We focus attention on the gas carbon dioxide. The counter-current system of the choroid rete mirabile, acting as a counter-current multiplier and while secreting oxygen, in theory, must also accumulate carbon dioxide at its distal end. The theory of countercurrent multiplication in this system, proposed by W. Kuhn and his associates (Kuhn and Marti, 1966; Kuhn, Ramel, Kuhn and Marti, 1963), and recently somewhat amended (Alexander, 1966; Berg and Steen, 1968; Wittenberg and Wittenberg, 1974), is discussed by Wittenberg, Schwend and Wittenberg (1964), as it applies to carbon dioxide. During oxygen secretion, the carbon dioxide pressure in equilibrium with the capillaries at the distal end of a swim-bladder rete reaches 275 mm Hg or 0.37 atmosphere (Wittenberg *et al.*, 1964). If a similar situation were to occur in the eye, the concentration of carbon dioxide near the retina would be 13.5 millimolar [At 20° C and assuming the solubility of CO<sub>2</sub> in eye tissues is similar to that of blood plasma (Van Slyke, Sendroy, Hastings and Neill (1928).] At physiological pH, the carbon dioxide would be 90 per cent or more ionized, and the protons so generated might well overwhelm the local buffering capacity and be damaging to the tissue. We advance the suggestion that the pseudobranch acts to modify the ophthalmic arterial blood so as to prevent the accumulation of excessive carbon dioxide at the distal end of the choroid rete.

This suggestion immediately encounters a difficulty. In some species the pseudobranch is buried, and the degree to which it has access to ambient water, different in different species, is not yet established. Nonetheless there is strong evidence that buried pseudobranchs do act to modify the ionic composition of the ophthalmic arterial blood. The activity of sodium-potassium-activated adenosine triphosphatase (an enzyme implicated in ionic transport) is enhanced tenfold in the buried pseudobranch of *Fundulus* maintained in sea water relative to the fresh water controls (Epstein, Katz and Pickford, 1967). Conceivably material exchange in the buried pseudobranch occurs, not with seawater, but with the systemic blood of surrounding tissues. We put this difficulty aside for the moment, and return to the question of what material may be exchanged.

Total removal of carbon dioxide and bicarbonate anion from the ophthalmic arterial blood will not do, although decreasing their concentration might be helpful. An essential point in the operation of the countercurrent multiplier is the conservation of protons generated within the system. Carbon dioxide is required to serve as a mobile carrier of protons across the capillary wall from the outgoing to the incoming blood stream.

Secondly, the chemical composition of the blood of fresh and salt-water fishes (Holmes and Donaldson, 1969) gives no clue as to why fresh water fish alone may dispense with the pseudobranch. The total carbon dioxide contents of the blood of fresh and salt-water teleosts fall within the same range (4–10 millimoles per liter).

An attractive possibility is that the pseudobranch might effect a forced exchange of blood bicarbonate ion for external chloride ion. Such a process is described by Maetz and Romeu (1964) (Romeu and Maetz, 1964) in the gill of the goldfish; it depends on carbonic anhydrase. The pseudobranch of a marine fish carrying out a bicarbonate/chloride exchange could reduce total blood carbon dioxide to a level which when multiplied in the counter-current system would not be damaging.

In fresh water, such exchange would be limited by the available chloride, and the pseudobranch could be dispensed with, as it has been in some groups.

We discuss next the role of carbonic anhydrase in oxygen secretion. Carbonic anhydrase occurs in massive concentration in all structures involved in oxygen secretion. These include the pseudobranch (Hoffert, 1966; Leiner, 1940; Leiner and Leiner, 1940; Maetz, 1956; Sobotka and Kann, 1941), the choroid rete mirabile (Hoffert, 1966; Leiner, 1939, 1940; Leiner and Leiner, 1940; Maetz, 1956), the pigment cell layer of the teleost retina (Leiner, 1939; Maetz, 1956), the swimbladder rete mirabile (Fänge, 1950, 1966; Maren, 1962), and the gas gland of the swimbladder (Fänge, 1953). Significantly, the pseudobranch of elasmobranchs, which have no choroid rete, lacks this enzyme (Leiner, 1939).

The specific inhibitor of carbonic anhydrase, diamox, when administered to trout, *Salmo gairdneri*, abolishes active secretion of oxygen into the eye (Fairbanks, Hoffert and Fromm, 1969). Gas secretion into the swimbladder is also depressed by inhibitors of carbonic anhydrase (Fänge, 1950, 1953; Maetz, 1956). The primary actions of the carbonic anhydrase inhibitors cannot be other than multiple, effecting each of the array of structures involved in gas secretion and in addition effecting also the kinetics of gas exchange in the red blood cells (Berg and Steen, 1968) both at the gill and at the two retia. Lactate production by the swimbladder gas gland is inhibited by inhibition of carbonic anhydrase (Kutchai, 1971). Furthermore, it should be borne in mind that carbonic anhydrase accelerates not only the reaction for which it is named but is involved also in transcellular transport of ions (Keynes, 1969; Maren, 1967a, 1967b; Carter, 1972). The effect of the loss of carbonic anhydrase activity on the ionic environment of the retina may be distinguished from the many other effects, following the penetrating analysis developed by Maren (1967b).

Inhibition of carbonic anhydrase of the red blood cells markedly slows carbon dioxide exchange at the gill and thereby more than doubles the partial pressure of carbon dioxide in the blood (Hoffert and Fromm, 1966; Maren, 1967b). Since the gas diffuses freely through tissue, the  $p\text{CO}_2$  is everywhere increased. The events in the absence of counter-current exchange or multiplication may be inferred from the events at the ciliary body, a structure whose epithelium shares a common embryological origin with the pigment cell epithelium of the retina. Diamox inhibits formation of bicarbonate ion from blood-borne carbon dioxide at the ciliary body (Maren, 1967b); the bicarbonate concentration of the aqueous is thereby diminished (Hoffert and Fromm, 1966; Maren, 1962), and as already noted, the partial pressure of carbon dioxide is elevated. The result is a more acid pH. In the trout, the change is from a normal value of pH 7.65 to pH 7.22 (Hoffert and Fromm, 1966).

The counter-current system of the choroid rete mirabile would be expected to multiply a locally generated increment in carbon dioxide pressure many fold. This increment, the "single concentrating effect" (Kuhn and Marti, 1966; Kuhn, *et al.*, 1963), at least in the swimbladder rete, is the generation of carbon dioxide from blood borne bicarbonate anion (Wittenberg *et al.*, 1964) through the action of lactic acid added to the blood locally. The amount of blood bicarbonate ion available may limit the magnitude of the increment (Wittenberg *et al.*, 1964). If diamox,

by interfering with pseudobranchial function, causes the local blood bicarbonate ion concentration to rise, the carbon dioxide pressure generated by the "single concentrating effect" will also rise. The counter-current multiplication effect in the choroid rete mirabile would be expected to multiply this larger pressure increment several fold with a consequent large fall in pH, at the distal end of the system. This expectation is borne out in a crucial experiment reported by Maetz (1956), who measured the pH of the vitreous humor adjacent to the retina of perch. Normally the pH of the vitreous is pH 7.6, slightly alkaline to the blood plasma (pH 7.45). Following administration of diamox, the pH of the vitreous fell precipitously, more than 0.5 unit, to pH 6.9-7.1 within an hour. In the ensuing twelve hours, it fell nearly as much again, to reach pH 6.6. This acidity was sufficient to destroy the retina, and the animals became blind. The pH is that expected of a weakly buffered, strong solution of carbonic acid. The pressure of carbon dioxide must be very elevated.

In this experiment, diamox accentuated an effect inherent in the operation of a counter-current system, multiplication of the concentration of the diffusible carbon dioxide which, when hydrated, becomes a strong acid. Maetz's result strengthens our contention that the pseudobranch acts in consort with the choroid rete mirabile to create a high oxygen concentration at the retina without simultaneously accumulating an excessive concentration of carbon dioxide.

Thus, our findings combined with those of others lead to a working hypothesis for a function of the pseudobranch. A virtue of the hypothesis is that it may be put to the test of experiment. That experiment is to measure and compare ionic exchanges in the pseudobranchs of marine and fresh-water fishes.

We wish to thank the many people who have helped us in the course of this work; in particular, Dr. Donn E. Rosen and Dr. Gareth J. Nelson for their continuing advice, helpful discussion and for access to specimens in the collections of the American Museum of Natural History. We also thank Dr. D. Eugene Copeland for discussion of the anatomy of the pseudobranch, Dr. Ole Munk whose observations on the occurrence of the choroid rete we have quoted extensively, Dr. N. A. Locket for permission to quote his unpublished observations, Mrs. Myvanwy M. Dick for access to the collections of Museum of Comparative Zoology, Harvard University, Miss J. M. Reinhart for access to the collections of the Systematics and Ecology Program, Marine Biological Laboratory, Woods Hole, and the staff of the Supply Department, Marine Biological Laboratory for their help. We are also grateful to the many people who, over the years, have provided us with occasional rare specimens, particularly R. McN. Alexander, F. G. Carey, H. W. Klimm, G. Fahlén, R. Forster, P. H. Greenwood, K. Johansen, K. Liem, K. S. Thompson, C. Wheeler, F. G. Wood. Histological preparations were made by N. R. Rothman, A. Scorza and R. Meyer.

#### SUMMARY

The choroid rete mirabile is a vascular counter-current organ located behind the retina of the eye and responsible in part for the maintenance of a high partial pressure of oxygen there. It is absent in cyclostomes, elasmobranchs, and all living



non-teleost bony fishes with the exception of the holostean, *Amia calva*. The choroid rete is found widely distributed among teleosts and is nearly always present in the Acanthopterygii, which comprise the great majority of living forms. The ability to do without a choroid rete typifies families or orders, but is a character of limited phyletic usefulness. There seems little correlation between habitat and presence or absence of the choroid rete. The choroid rete and the rete mirabile of the swimbladder occur independently. This does not seem to be true for the choroid rete and the pseudobranch, since almost all fishes which have a choroid rete also have a pseudobranch. Arterial blood comes to the choroid rete mirabile by way of the pseudobranch, and those instances in which the latter is lost offer an occasion for deductions about its function. We argue that the pseudobranch acts to modify the incoming arterial blood in such a way that the choroid rete may concentrate oxygen without simultaneously concentrating carbon dioxide, which when hydrated becomes a strong acid.

## LITERATURE CITED

- ALEXANDER, R. M., 1966. Physical aspects of swimbladder function. *Biol. Rev.*, **41**: 141-171.
- ALLEN, W. F., 1905. The blood-vascular system of the Loricati, the mail-checked fishes. *Proc. Nat. Acad. Sci.*, **7**: 27-157.
- ALLIS, E. P., 1900. The pseudobranchial circulation in *Amia calva*. *Zool. Jahrb. Anat.*, **14**: 107-134.
- ALLIS, E. P., 1908. The pseudobranchial and carotid arteries in the gnathostome fishes. *Zool. Jahrb. Anat.*, **27**: 103-134.
- ALLIS, E. P., 1912. The pseudobranchial and carotid arteries in *Esox*, *Salmo* and *Gadus*, together with a description of the arteries in the adult *Amia*. *Anat. Anz.*, **41**: 113-142.
- AMERICAN FISHERIES SOCIETY, 1960. *A List of Common and Scientific Names of Fishes from the United States and Canada*. [Second Edition] Waverly Press, Baltimore, Maryland, 87 pp.
- BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, D. L. SHORES, J. M. TEAL, A. S. WING, G. W. MEAD AND W. D. CLARKE, 1968. *Ceratoscopelus maderensis*: Peculiar sound-scattering layer identified with this myctophid fish. *Science*, **160**: 991-993.
- BARNETT, C. H., 1951. The structure and function of the choroidal gland of teleostean fish. *J. Anat.*, **85**: 113-119.
- BERG, T., AND J. B. STEEN, 1968. The mechanism of oxygen concentration in the swimbladder of the eel. *J. Physiol.*, **195**: 631-638.
- BERTELSEN, E., B. THEISEN AND O. MUNK, 1965. On a postlarval specimen, anal light organ and tubular eyes of the argentinoid fish *Rhynchohyalus natalensis* (Gilchrist and von Bonde). *Vidensk. Meddr. Dansk Naturh. Foren.*, **128**: 357-371.
- BIGELOW, H. B. AND W. C. SCHROEDER, 1953. *Fishes of the Gulf of Maine*. United States Government Printing Office, Washington, 1953 (reprinted, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 1964).
- BRAUER, A., 1902. Über den Bau des Auges einiger Tiefseefische. *Verh. Deutsch. Zool. Gesell.*, **11**: 42-57.
- BRAUER, A., 1908. Die Tiefseefische, 2. *Anat. Teil. Wiss. Ergebn. Valdivia Reports*, **15**: 1-266.
- CARTER, M. J., 1972. Carbonic anhydrase: isoenzymes, properties, distribution, and functional significance. *Biol. Rev.*, **47**: 465-513.
- COPELAND, D. E., 1951. Function of glandular pseudobranch in teleosts. *Amer. J. Physiol.*, **167**: 755 (Abstr.).
- COPELAND, D. E. AND A. J. DALTON, 1958. An association between mitochondria and the endoplasmic reticulum in the cells of the pseudobranch gland of a teleost. *J. Biophys. Biochem. Cyt.*, **5**: 393-396.
- DUKE-ELDER, S., 1958. The Eye in Evolution. Page 300 in S. Duke-Elder, Ed., *System of Ophthalmology*, Volume I. C. V. Mosby Company, St. Louis.

- EPSTEIN, F. H., A. I. KATZ AND G. E. PICKFORD, 1967. Sodium- and potassium-activated adenosine triphosphatase of gills: Role in adaptation of teleosts to salt water. *Science*, **156**: 1245-1247.
- FAHLÉN, G., 1967a. Morphological aspects on the hydrostatic function of the gas bladder of *Clupea harengus* L. *Acta Univ. Lund.*, Section II, Number 1: 1-49.
- FAHLÉN, G., 1967b. Morphology of the gas bladder of *Coregonus lacarectus* L. *Acta Univ. Lund.*, Section II, Number 28: 1-37.
- FAHLÉN, G., 1968. The gas bladder as a hydrostatic organ in *Thymallus thymallus* L., *Osmerus operlanus* L. and *Mallotus villosus* Müll. *Fisk Dir. Skr. Ser. HavUnders.*, **14**: 199-228.
- FAIRBANKS, M. B., J. R. HOFFERT, AND P. O. FROMM, 1969. The dependence of the oxygen-concentrating mechanism of the teleost eye (*Salmo gairdneri*) on the enzyme carbonic anhydrase. *J. Gen. Physiol.*, **54**: 203-211.
- FÄNGE, R., 1950. Carbonic anhydrase and gas secretion in the swimbladder of fishes. *XI/III International Physiol. Congr.*, **1950**: 192-193.
- FÄNGE, R., 1953. The mechanisms of gas transport in the euphysoclist swimbladder. *Acta Physiol. Scand.*, **30** (suppl. 110): 1-133.
- FÄNGE, R., 1958. The structure and function of the gas bladder in *Argentina silus*. *Quart. J. Microscop. Sci.*, **99**: 95-102.
- FÄNGE, R., 1966. The physiology of the swimbladder. *Physiol. Rev.*, **46**: 299-322.
- FÄNGE, R. AND A. MATTISSON, 1956. The gas secretory structures and the smooth muscles of the swimbladder of cyprinids. Pages 153-162 in K. G. Wingstrand, Ed., *Bertil Hanström zoological papers in honour of his sixty-fifth birthday*. Zoological Institute, Lund, Sweden.
- FÄNGE, R. AND J. B. WITTENBERG, 1958. The swimbladder of the toadfish (*Opsanus tau* L.). *Biol. Bull.*, **115**: 172-179.
- GOODRICH, E. S., 1930. *Studies on the Structure and Development of Vertebrates*. MacMillan and Co., London (reprinted Dover Publications, New York, 1958).
- GRANEL, F., 1922. Signification morphologique de la pseudobranchie des téléostéens. *C. R. Acad. Sci. Paris*, **175**: 349-351.
- GREENWOOD, P. H., G. S. MYERS, D. E. ROSEN AND S. H. WEITZMAN, 1967. Named main divisions of teleostean fishes. *Proc. Biol. Soc. Washington*, **80**: 227-228.
- GREENWOOD, P. H. AND D. E. ROSEN, 1971. Notes on the structure and relationships of the alepocephaloid fishes. *American Museum Novitates*, No. **2473**, 1-41.
- GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN AND G. S. MYERS, 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History (New York)*, **131**: 339-456.
- HARB, J. M., 1969. Comparative fine structure of the acidophil cell of the pseudobranch and gill of three teleosts. *Ph.D. thesis, Tulane University*, New Orleans, 83 pp.
- HARB, J. M. AND D. E. COPELAND, 1969. Fine structure of the pseudobranch of the flounder *Paralichthys lethostigma*. *Z. Zellforsch.*, **101**: 167-174.
- HOFFERT, J. R., 1966. Observations on ocular fluid dynamics and carbonic anhydrase in tissues of the lake trout (*Salvelinus namaycush*). *Comp. Biochem. Physiol.*, **17**: 107-114.
- HOFFERT, J. R. AND P. O. FROMM, 1966. Effect of carbonic anhydrase inhibition on aqueous humor and blood bicarbonate ion in the teleost (*Salvelinus namaycush*). *Comp. Biochem. Physiol.*, **18**: 333-340.
- HOLMES, W. N. AND E. M. DONALDSON, 1969. *The body compartments and distribution of electrolytes*. Pages 1-89 in W. S. Hoar and D. J. Randall, Eds., *Fish Physiology*, Vol. I. Academic Press, Inc., New York.
- KANWISHER, J. AND A. EBELING, 1957. Composition of the swimbladder gas in bathypelagic fishes. *Deep Sea Research*, **4**: 211-217.
- KEYNES, R. D., 1969. From frog skin to sheep rumen: a survey of transport of salts and water across multicellular structures. *Quart. Rev. Biophys.*, **2**: 177-281.
- KUHN, H. J. AND E. MARTI, 1966. The active transport of oxygen and carbon dioxide into the swimbladder of fish. *J. Gen. Physiol.*, **49**: 1209-1220.
- KUHN, W., A. RAMEL, H. J. KUHN AND E. MARTI, 1963. The filling mechanism of the swimbladder. Generation of high gas pressures through hairpin counter-current multiplication. *Experientia*, **19**: 497-511.

- KUTCHAI, H., 1971. Role of carbonic anhydrase in lactate secretion by the swimbladder. *Comp. Biochem. Physiol.*, **39A**: 357-359.
- LAURENT, P., 1967. Le pseudobranchie des téléostéens: preuves électrophysiologique de ses fonctions, chémoréceptrice et baroréceptrice. *C. R. Acad. Sci. Paris*, **264**: 1879-1882.
- LAURENT, P. AND S. DUNEL, 1964. L'innervation de la pseudobranchie chez la Tanche. *C. R. Acad. Sci. Paris*, **258**: 6230-6233.
- LAURENT, P. AND S. DUNEL, 1966. Recherches sur l'innervation de la pseudobranchie des téléostéens. *Archs. Anat. Microsc.*, **55**: 633-656.
- LEINER, M., 1939. Die Augenkienendrüse (Pseudobranchie) der Knochenfische. *Z. Vergh. Physiol.*, **26**: 416-466.
- LEINER, M., 1940. Das Atmungsferment Kohlendäureanhydratase im Tierkörper. *Naturwissenschaften*, **28**: 165-171.
- LEINER, M. AND G. LEINER, 1940. Das Ferment Kohlendäureanhydratase im Tierkörper. *Biol. Zentr.*, **60**: 449-472.
- MAETZ, J., 1956. Le rôle biologique de l'anhydrase carbonique chez quelques téléostéens. *Bull. Biol. France, Belgique (Paris)*, Supplement **40**: 1-129.
- MAETZ, J. AND F. G. ROMEU, 1964. The mechanism of sodium and chloride uptake by the gills of a fresh-water fish, *Carassius auratus*. II. Evidence for  $\text{NH}_4^+/\text{Na}^+$  and  $\text{HCO}_3^-/\text{Cl}^-$  exchanges. *J. Gen. Physiol.*, **47**: 1209-1227.
- MAREN, T. H., 1962. Ionic composition of cerebrospinal fluid and aqueous humor of the dog-fish, *Squalus acanthias*. II. Carbonic anhydrase activity and inhibition. *Comp. Biochem. Physiol.*, **5**: 201-215.
- MAREN, T. H., 1967a. Carbonic anhydrase in the animal kingdom. *Fed. Proc.*, **26**: 1097-1103.
- MAREN, T. H., 1967b. Carbonic anhydrase, chemistry, physiology and inhibition. *Physiol. Rev.*, **47**: 595-781.
- MARSHALL, N. B., 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery Reports*, **31**: 1-122.
- MCDOWELL, S. B., 1973. Order Heteromi (Notacanthiformes). Pages 1-228 in *Fishes of the Western North Atlantic*. Sears Foundation for Marine Research, Bingham Laboratory, Yale University, Memoir I, Number 6.
- MILLOT, J. AND J. ANTHONY, 1958a. *Latimeria chalumnae*, dernier des Crossoptérygiens. Pages 2553-2597 in P. Grasse, Ed., *Traité Zoologie*, Tome 13. Masson, Paris.
- MILLOT, J. AND J. ANTHONY, 1958b. *Anatomie de Latimeria chalumnae, Tome I, Squelette, Muscles et Formations de Soutien*. Éditions du Centre National de la Recherche Scientifique, Paris.
- MILLOT, J. AND J. ANTHONY, 1965. *Anatomie de Latimeria chalumnae, Tome II, Système Nerveux et Organes des Sens*. Éditions du Centre National de la Recherche Scientifique, Paris.
- MILLOT, J. AND N. CARASSO, 1955. Note préliminaire sur l'oeil de *Latimeria chalumnae*. *C. R. Acad. Sci.*, **241**: 576-583.
- MÜLLER, J., 1839. Vergleichende Anatomie der Myxinoiden: Über das Gefässsystem. *Abh. Berlin Akad.*, **1839**: 175-303.
- MUNK, O., 1964. The eye of *Calamioichthys calabaricus* Smith, 1865 (Polypteridae, Pisces) compared with the eye of other fishes. *Vidensk. Meddr. Dansk Foren.*, **127**: 113-126.
- MUNK, O., 1965. *Omosudis Loweii* Günther, 1887, a bathypelagic deep-sea fish with an almost pure cone retina. *Vidensk. Meddr. Dansk Naturh. Foren.*, **128**: 341-355.
- MUNK, O., 1966a. Ocular anatomy of some deep-sea teleosts. *Dana Report*, **70**: 1-62.
- MUNK, O., 1966b. On the retina of *Diretmus argenteus*, Johnson, 1863 (Diretmidae, Pisces). *Vidensk. Meddr. Dansk. Naturh. Foren.*, **129**: 73-80.
- MUNK, O., 1968a. On the eye and the so-called preorbital light organ of the isospondylous deep-sea fish *Bathylaco nigricans* Goode and Bean, 1896. *Galathea Report*, **9**: 211-238.
- MUNK, O., 1968b. The eyes of *Amia* and *Lepisosteus* (Pisces, Holostei) compared with the brachiopterygian and teleostean eyes. *Vidensk. Meddr. Dansk Naturh. Foren.*, **131**: 109-127.
- MUNK, O., 1969a. The eye of the "four-eyed" fish *Dialommus fuscus* (Pisces, Blennioidei, Clinidae). *Vidensk. Meddr. Dansk Naturh. Foren.*, **132**: 7-24.
- MUNK, O., 1969b. On the visual cells of some primitive fishes with particular regard to the classification of rods and cones. *Vidensk. Meddr. Dansk Naturh. Foren.*, **132**: 25-30.

- MUNK, O., 1970. On the occurrence and significance of horizontal band-shaped retinal areas in teleosts. *Vidensk. Meddr. Dansk Naturh. Foren.*, **133**: 85-120.
- NELSON, G. J., 1969a. Origin and diversification of teleostean fishes. *Ann. New York Acad. Sci.*, **167**: 18-30.
- NELSON, G. J., 1969b. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History (New York)*, **141**: 475-552.
- POERNOMO, A., 1967. Notes on the pseudobranchiae of cyprinodontidae, subfamilies rivulinae, procatopodinae and lamprichthyinae. *Vidensk. Meddr. Dansk Naturh. Foren.*, **130**: 109-116.
- PRINCE, J. H., 1956. *Comparative Anatomy of the Eye*. Charles C. Thomas Co., Springfield, Illinois, 246 p.
- RICHARD, J., 1895. Sur les gaz de la vessie nataoire de poissons. *C. R. Acad. Sci.*, **120**: 745-747.
- RITCH, R. AND C. W. PHILPOTT, 1969. Repeating particles associated with an electrolyte-transport membrane. *Exp. Cell Res.*, **55**: 17-24.
- ROMEU, F. G. AND J. MAETZ, 1964. The mechanism of sodium and chloride uptake by the gills of a fresh-water fish, *Carassius auratus*. I. Evidence for an independent uptake of sodium and chloride ions. *J. Gen. Physiol.*, **47**: 1195-1207.
- ROSEN, D. E. AND P. H. GREENWOOD, 1970. Origin of the weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. *American Museum Novitates*, Number **2428**, 1-25.
- ROSEN, D. E. AND C. PATTERSON, 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History (New York)*, **141**: 357-374.
- ROSS, D. M., 1963. The sense organs of *Myxine glutinosa* L. Pages 150-160 in A. Brodal and R. Fänge, Eds., *The Biology of Myxine*. Universitetsforlaget, Oslo.
- RUDD, J. T., 1965. The Ice Fish. *Sci. Amer.*, **213** (November): 108-114.
- SCHLOESING, T. AND J. RICHARD, 1896. Recherche de l'argon dans le gaz de la vessie nataoire de poissons et des physalies. *C. R. Acad. Sci.*, **122**: 615-617.
- SOBOTKA, H. AND S. KANN, 1941. Carbonic anhydrase in fishes and invertebrates. *J. Cell. Comp. Physiol.*, **17**: 341-348.
- SUNDNES, G., 1963. Studies on the high nitrogen content in the physostome swimbladder. *Fisk Dir. Skr. Ser. HavUnders.*, **13** (5): 1-8.
- TYLER, J. C., 1960. Erythrocyte counts and hemoglobin determinations for two antarctic nototheniid fishes. *Stanford Ichthyological Bulletin*, **7** (4): 199-201.
- VAN SLYKE, D. D., J. SENDROY, A. B. HASTINGS AND J. M. NEILL, 1928. Studies of gas and electrolyte equilibria in blood. X. The solubility of carbon dioxide at 38° in water, salt solution, serum and blood cells. *J. Biol. Chem.*, **78**: 765-799.
- WALLS, G. L., 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Cranbrook Inst. Sci. Bull. No. 19, Michigan, 785 pp. [Reprinted Hainer Publishing Co., Inc., New York, 1963].
- WITTENBERG, J. B., 1958. The secretion of inert gas into the swimbladder of fish. *J. Gen. Physiol.*, **41**: 783-804.
- WITTENBERG, J. B., M. J. SCHWEND AND B. A. WITTENBERG, 1964. The secretion of oxygen into the swimbladder of fish. III. The role of carbon dioxide. *J. Gen. Physiol.*, **48**: 337-355.
- WITTENBERG, J. B. AND B. A. WITTENBERG, 1962. Active secretion of oxygen into the eye of fish. *Nature*, **194**: 106-107.
- WITTENBERG, J. B. AND B. A. WITTENBERG, 1974. The choroid rete mirabile of the first eye. I. Oxygen secretion and structure. *Biol. Bull.*, **146**: 116-136.